Growth of male and female *Araucaria araucana* trees respond differently to regional mast events, creating sex-specific patterns in their tree-ring chronologies

Martín A. Hadad[1]*; Fidel A. Roig[2,3]; Julieta G. Arco Molina[2]; Andrew Hacket-Pain[4]

[1]Laboratorio de Dendrocronología de Zonas Áridas CIGEOBIO (CONICET-UNSJ), Gabinete de Geología Ambiental (INGEO-UNSJ), San Juan, Argentina.

[2]Laboratorio de Dendrocronología e Historia Ambiental, IANIGLA-CCT CONICET-Universidad Nacional de Cuyo, Mendoza, Argentina.

[3]Hémera Centro de Observación de la Tierra, Facultad de Ciencias, Universidad Mayor, Huechuraba, Santiago, Chile.

[4]Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, L697ZT, UK.

*e-mail: mhadad@unsj-cuim.edu.ar

Abstract

Araucaria araucana is a dioecious evergreen conifer endemic to temperate forests of south Argentina and Chile. It is a long-lived species (maximum age >1000 years), and it presents a high potential for tree-ring based climate reconstructions. However, the species' dioecious habit can result in distinct sex-specific growth patterns, which introduce novel challenges in the interpretation of tree-ring chronology variations. We used a network of 10 tree-ring chronologies from northwest Patagonia (Argentina) to analyze sex-specific growth patterns in *A. araucana* and, for the first time, demonstrate that they result from the contrasting responses of ring width index of male (RWI_{male}) and female (RWI_{female}) trees to regional mast events (years with high seed production). During the year of seed maturation and seed dispersal, the growth of females is strongly and significantly reduced, while a growth response of similar magnitude was found in

male trees in the previous year, corresponding to the year of pollination. We interpret these growth responses as representing contrasting allocation shifts between growth and reproduction in males and females. The sex-specific growth responses associated with mast events resulted in a particularly strong and distinct signal in a RWI_{male}–RWI_{female} chronology. Male and female tree-ring chronologies share a strong common signal, and respond similarly (but not exactly) to broad-scale climatic conditions in the growing season. Our results indicate that sex-specific tree-ring chronologies can be used to isolate mast events in *A. araucana* chronologies, providing an opportunity to develop unique multi-century reconstructions of large mast events, and improve dendroclimatic calibration for this species.

Keywords: carbon allocation; dendroecology; trade-off; dendroclimatology; Patagonia.

1. Introduction

Araucaria araucana (Molina) K. Koch is a long-lived (maximum age >1000 years) dioecious conifer endemic from temperate forests of south Argentina and Chile (Roig and Villalba, 2008; Aguilera-Betti et al., 2017). Its importance for dendroecological and climatic studies is well documented (Mundo et al., 2012; Muñoz et al., 2014; Hadad et al., 2015, 2020; Hadad and Roig, 2016; Rozas et al., 2019), including for climate variability reconstructions (e.g. Villalba et al., 2012; Morales et al., 2020). Furthermore, large-scale atmospheric phenomenon have been detected in *A. araucana* tree rings, evidenced by the link between its growth responses and the sea surface temperature (SST) anomalies of the Niño 3.4 region in the tropical Pacific Ocean, and with the atmospheric pressure differences between the middle and high latitudes (~40°- 65°S) of the Southern Hemisphere, represented by the Southern Annular Mode (SAM) index

(Mundo et al., 2012; Villalba et al., 2012; Hadad et al., 2015; Hadad and Roig, 2016; Morales et al., 2020). Analysis of stable carbon isotopes of *A. araucana* tree rings has also provided information on the long-term physiological reaction of this endangered species (International Union for Conservation of Nature, http://www.iucnredlist.org/) to recent climate changes, as evidenced by the increase in intrinsic water-use efficiency (iWUE) during recent decades (Arco Molina et al., 2019).

Dendroclimatic reconstructions are dependent on a strong and stable relationship between growth and climate (Fritts, 1976). However, the physiological mechanisms linking climate and growth are complex, and include the effects of resource assimilation and allocation, among others, which vary at interannual timescales (Thomas, 2011). This can reflect adaptive responses to stress (Lauder et al., 2019), or result from a potential trade-off or switching of resources in years of high investment in reproduction (Selas et al., 2002; Monks and Kelly, 2006; Hacket-Pain et al., 2018). The effects of dynamic resource allocation is particularly important in masting species, which are characterized by highly variable allocation to reproduction (Kelly, 1994). Years of high investment in reproduction (mast events) represent a major sink of carbon and other resources. For example, Müller-Haubold et al. (2013) showed that in central European beech forests, carbon allocation to reproduction varied between 2-50% of total aboveground Net Primary Production between non-mast and mast events. Negative relationships between growth and reproduction have been reported in many species (Norton and Kelly, 1988; Selas et al., 2002; Hacket-Pain et al., 2018; Lauder et al., 2019), although the nature of this apparent trade-off has been questioned in those cases where carbon resources do not appear to limit tree growth (Mund et al., 2020). Nevertheless, variable allocation of resources to reproduction explains an important

component of year-to-year variability in tree growth (Monks and Kelly, 2006; Müller-Haubold et al., 2013, Hacket-Pain et al., 2018).

Araucaria araucana provides a valuable opportunity to improve understanding of the relationship between reproduction and growthby taking advantage of within-species sex-specific allocation to reproduction (Obeso, 2002). Previous studies in other dioecious species (e.g. *Juniperus communis* subsp. *alpina* (Suter) Celak; *Ilex aquifolium* L.) have indicated that investment in reproduction is higher in female trees, leading to a long-term reduction in female growth relative to males (Obeso, 2002; Ortiz et al., 2002). However, the potential effect of reproduction on interannual growth variation remains largely unexplored. *A. araucana* presents a further advantage as its reproductive cycle crosses multiple years, with pollination and seed maturation occurring in different years (Fig. 1). Consequently, we hypothesize that the costs of reproduction for male and female *A. araucana* trees are concentrated within different years. Costs associated with reproduction in females occur mainly in the year of cone maturation (t), while the costs for males occur mainly in the year of pollination (t-1) (Fig. 1). We further hypothesize that these sex-specific costs of reproduction, coupled with a growth-reproduction trade-off (Rozas et al., 2019) and a highly variable reproductive effort between years (Sanguinetti and Kitzberger, 2008; Sanguinetti, 2014), may explain previously reported differences in growth variability between sexes in *Araucaria araucana* (Hadad and Roig, 2016; Rozas et al., 2019). Further, this work aims at testing the relationship between tree-ring chronologies and sea surface temperature to evaluate the climate sensitivity of male and female tree growth.

2. Materials and Methods

2.1 Timeline of seed production in *A. araucana*

A. araucana is a masting species, and previous studies have indicated that moderate to large cone and seed crops ("mast events") occur every 2-5 years (Montaldo, 1974; Donoso et al., 2006; Sanguinetti and Kitzberger, 2008). The largest mast events are associated with cone production >2 standard deviations from the long-term mean, and occur synchronously across the restricted geographic distribution of the species (Sanguinetti and Kitzberger, 2008). As the *A. araucana* pollen grain is one of the largest pollen grains (80-100 μm in diameter) among all conifers (Huesser et al., 1988; Owens et al., 1998), synchronization of large-scale flowering may help to alleviate pollen limitation (Pearse et al., 2016).

Preliminary observations of *A. araucana* reproductive biology indicate that the primordia of the pollen cones (male) is already formed during the austral fall, while the archesporium is differentiated in winter months, remaining in this stage until mid-October (Del Fueyo et al., 2008). Towards early summer, the pollen grains are mature, and pollination takes place (Del Fueyo et al., 2008; Donoso et al., 2009). Therefore, the microsporangiate strobili or pollen cones (males) can complete their cycle in almost eight months while the megasporangiate strobili or seed cones (females) take more than a year to complete their maturity (Del Fueyo, pers. com.), with seed fall occurring in late summer or early autumn (February-March) of the following year (Fig. 1).

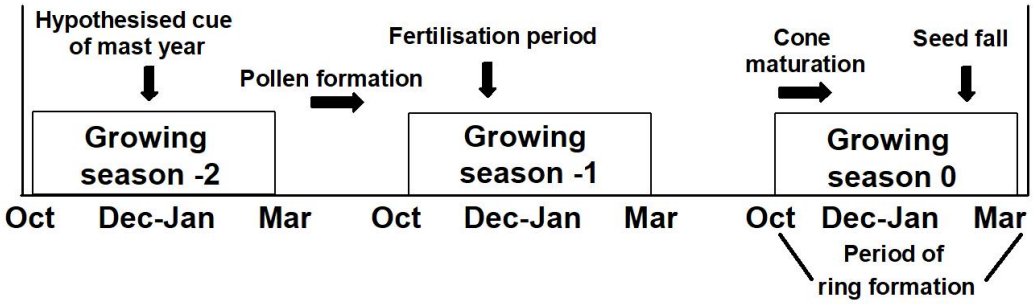


Figure 1: Hypothesised cue of mast years and timeline of *Araucaria araucana* male and female cone maturation.

2.2. Study sites

Ten stands of *A. araucana* trees (four xeric and six mesic forests) located in northwestern Patagonia, Argentina, were studied (Fig. 2, Table 1). The region is characterized by a strong precipitation gradient from west to east, with higher annual precipitation at the Andes cordillera and lower towards the steppe. The xeric sites are distributed in an area with a mean annual temperature of 11.1 °C (reference period 1912-2005) and a total annual precipitation around 573 mm (period 1929-2001). Mean climate at the mesic sites is cooler and wetter, with a mean annual temperature of 8.7 °C (period 1912-2008) and a total annual precipitation of around 1081 mm (period 1931-2010) (Hadad et al., 2020).

In the field, two or three increment wood cores per tree were taken at breast height (1.3 m above ground level) with an increment borer of 5 mm diameter for both female and male *A. araucana* trees. All cores were taken from single-stemmed living trees and from trunk portions without cracks, branches, reaction wood, or other growth anomalies that could hinder the tree ring identification and measurement. The sex of the trees was established by observing with binoculars the presence and type (female/male)

of the strobiles (Fig. 3AB). We did not sample trees that could not be unambiguously sexed. A set of 66 (74) female (male) trees were sampled in the xeric forests, while 47 (47) female (male) trees were sampled from the mesic sites (Table 1). The sexual ratio of these sites was close to 1:1 (Hadad et al., 2020).

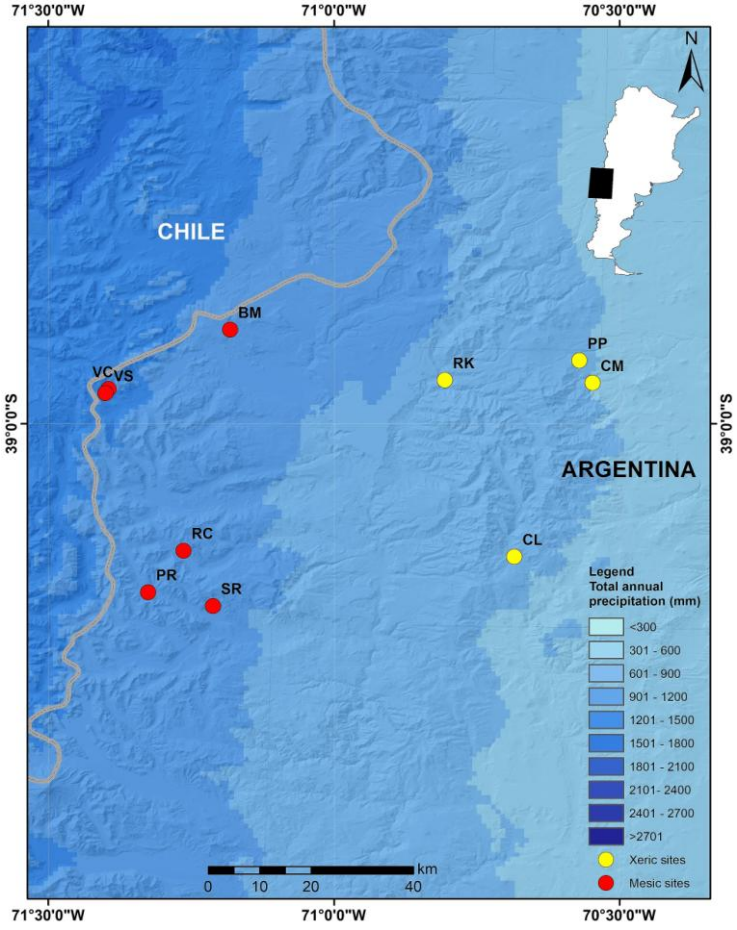


Figure 2: Xeric (yellow dots) and mesic (red dots) study sites from northwestern Patagonia, Argentina (site codes are shown in Table 1). The relative position of the study area is marked as a black rectangle on the inset outline of Argentina. The precipitation gradient from 1970 to 2000 (Fick and Hijmans, 2017) is also shown..

Table 1: Characteristics of the sampled sites and chronology statistics.

Forest type	Site (Code)	Latitude S	Longitude W	Altitude	Sex/N° of trees	Chronology span	Rbar	Start (EPS >0.85)
Xeric	Primeros Pinos (PP)	38º 52'	70º 34'	1628	Female/18	1528-2008	0.309	1705
					Male/16	1277-2008	0.260	1730
	Río Kilca (RK)	38º 53' ''	70º 50'	1442	Female/15	1190-2013	0.337	1875
					Male/7	1490-2013	0.270	1875
	Carreri Malal (CM)	38º 55'	70º 32'	1510	Female/12	1592-2010	0.292	1875
					Male/20	1421-2010	0.271	1805
	Catan Lil (CL)	39° 14'	70° 40'	1290	Female/10	1600-2011	0.307	1860
					Male/25	1631-2011	0.380	1750
Mesic	Batea Mahuida (BM)	38º 50'	71º 10'	1598	Female/10	1553-2012	0.351	1830
					Male/7	1628-2012	0.350	1780
	Valle El Salvo (VS)	38º 56'	71º 25'	1294	Female/8	1277-2012	0.359	1630
					Male//6	1271-2012	0.335	1705
	Verde Chico (VC)	38º 56'	71º 23'	1267	Female/11	1761-2013	0.346	1895
					Male/10	1716-2013	0.351	1870
	Rucachoroi (RC)	39° 13'	71° 15'	1214	Female/7	1648-2011	0.412	1725
					Male/10	1683-2011	0.401	1865
	Pinalada Redonda (PR)	39º 18'	71º 17'	1100	Female/5	1720-2013	0.303	1855
					Male/7	1626-2013	0.372	1750
	Senda a Rucachoroi (SR)	39º 19'	71º 12'	1507	Female/6	1305-2013	0.401	1885
					Male/7	1480-2013	0.446	1765

2.2. Laboratory work and chronology development

In the laboratory, the core samples were mounted on wooden supports and polished with progressively finer sandpaper to highlight the tree ring boundary structure (Stokes and Smiley, 1968, Fig. 3C). Ring widths were measured with a measuring device (Velmex, USA) , with a precision of 0.001 mm. The quality control of the measurements of the ring width series was checked with the COFECHA program (Holmes, 1983).

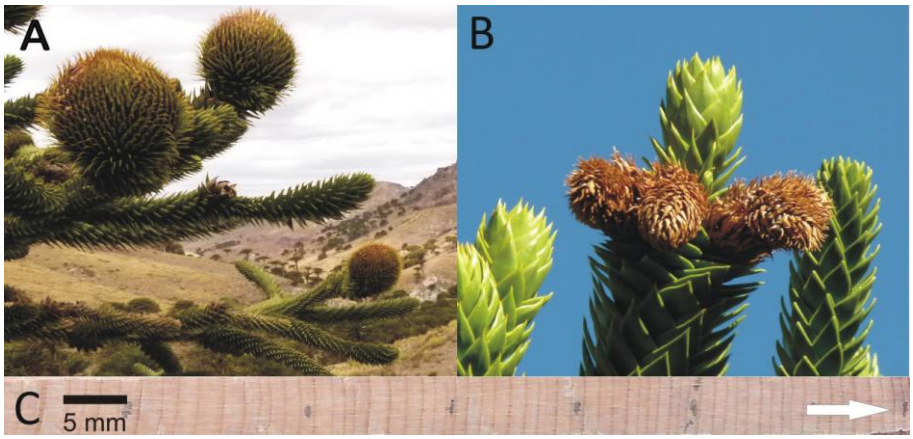


Figure 3: *Araucaria araucana* reproductive and wood features. A) a female tree with large and spherical seed cones; B) a male tree with sub-cylindrical, single, smaller pollen strobili on the tips of the canopy branches; C) a wood sample showing the annual tree ring pattern. The arrow indicates the direction towards the bark.

Raw ring width chronologies typically contain low-frequency (i.e., decadal and longer) signals associated with changes in tree age and size, canopy position and long-term changes in the environment (Fritts, 1976). In order to evaluate the relationship between annual growth and climate, this low-frequency variance was removed by detrending the raw ring width series using the R package 'dplR' (Bunn et al., 2019). Each series was fitted with a 50-year cubic spline with a 50% frequency cut off. Dimensionless ring width indices were created for each series by dividing the observed ring width by the fitted spline. Then, these individual ring width indices were averaged for each tree. Then, all sampled trees at each site were averaged to produce a mean site ring width index (RWI) chronology, and site-specific male and female chronologies using only male and female trees, respectively. We built regional chronologies by averaging the all-tree, male-only and female-only site chronologies. Additionally, we built site-specific and regional chronologies considering the difference between the RWI_{male} and RWI_{female} chronology (RWI_{male}-RWI_{female} chronologies). We used spatial

correlograms and a Mantel test to investigate the spatial correlation of tree growth across our network of study sites before averaging the individual 10 site chronologies into regional tree-ring chronologies. Mantel tests and correlograms were run with the R package 'ncf v1.1' (Bjornstad, 2015). We used Spearman's rank correlation as the measure of similarity between chronologies for the period between 1980 and the last common year shared by each pair of chronologies (2008-2013).

2.3. Sex-specific growth patterns

Sex-specific growth variability was assessed by comparing male and female chronologies at the individual, site, and regional level. At the individual-level a Principle Component Gradient Analysis (PCGA) (Buras et al., 2016) was used to characterize within-site growth variability, and to test whether the variability was related to tree sex. PCGA is based on principal component analysis and uses the polar-transformation of the loadings of the first and second principal components to identify population gradients or subpopulations (Buras et al., 2016). Sex-specific growth differences were tested using a Wilcoxon rank test of the angles of the polar coordinates of male and female trees from each site (Gut et al., 2019). Following the recommendation of Buras et al. (2018), tree-ring chronologies used for PCGA were separately detrended using autoregressive models. Detrending was performed using the R package 'dplR', with model selection to minimize Akaike's Information Criterion (the default option in the detrending function) (Bunn et al., 2018). PCGA analysis was conducted for a common overlap period for the trees sampled at each site. A small number of trees were excluded from PCGA at some sites as they were missing some outer tree rings.

2.4. Mast event identification

211 Mast events occur synchronously in *A. araucana* forests across the study region,
212 and large regional mast events occurred in 1995, 2000, 2007 and 2013 according to
213 Sanguinetti and Kitzberger (2008) and Sanguinetti (2014). As seed fall occurs in March
214 or April, and the tree ring formation starts in October or November of the previous
215 calendar year (Fig. 1), we re-dated the reported mast events to correspond to the
216 calendar year when the rings started forming (e.g. a mast event with seed fall recorded
217 April 1995 and dated to 1995 was re-dated to 1994 to correspond to the equivalent tree
218 ring, which started ring formation in October in 1994, and is consequently dated to
219 1994).

220 **2.5. Relationship between male and female tree-ring width and mast events**

221 Superposed Epoch Analysis (SEA) (Grissino-Mayer, 1995) was used to assess
222 the response of tree growth to mast events. SEA compares the mean growth before,
223 during and after an event with the mean growth of non-event years (Swetnam, 1993).
224 The significance of growth responses was estimated using a bootstrapping procedure
225 with 1,000 simulations (Bunn, 2008). Here, we used SEA to test growth responses of
226 male and female trees to known regional mast events by using the RWI chronologies,
227 testing the growth responses during the mast event and in a three-year window either
228 side of the event. We reported results for the regional RWI chronologies, and we
229 repeated the tests for sex-specific site chronologies (Appendix A). Additionally, we
230 applied SEA to a RWI_{male}-RWI_{female} chronology.

231 **2.6. Relationship between sex-specific tree growth and regional climate patterns**

232 To evaluate the spatial relationship between tree growth (female and male) and
233 broad-scale climate patterns, we compared regional RWI chronologies with Pacific sea
234 surface temperature (SST), and land surface temperatures. We used gridded monthly
235 SST and land surface data at a spatial resolution of 0.5° x 0.5° cells for the period 1948-

2013 originated from the NCEP re-analysis global dataset (Kalnay et al., 1996). The spatial correlation fields were performed using tools provided on the website of National Oceanic and Atmospheric Administration (NOAA/ESRL Physical Sciences Laboratory, Boulder Colorado, http://www.esrl.noaa.gov/psd/data/correlation/). Composite maps were created to evaluate the spatial features of spring-summer (Oct-Mar) SST anomalies in relation with tree growth for two years before the growing season (-2), for the previous growing season (-1) and for the current period of growth (0).

3. Results

3.1 Growth synchrony

Growth synchrony between sites was high (mean between-site rh0 = 0.49 male-only chronologies, rh0 = 0.38; female-only chronologies, rh0 = 0.49), and did not decline significantly with geographical distance across the study region, including for male- and female-only site chronologies (Mantel correlation = -0.13, p = 0.188; male-only chronologies = 0.08, p = 0.339; female-only chronologies = -0.20, p = 0.100. Fig. 4). These analyses indicated that it was appropriate to combine the 10 sites into a regional RWI chronology.

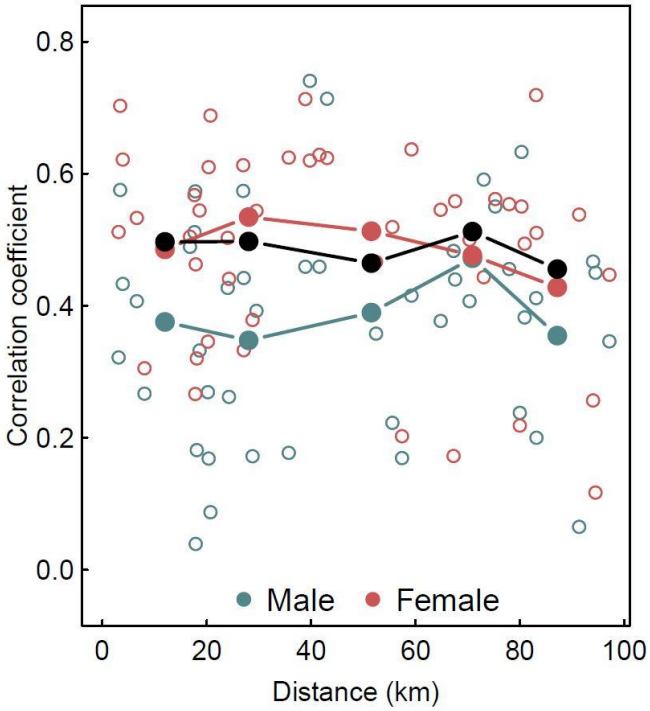
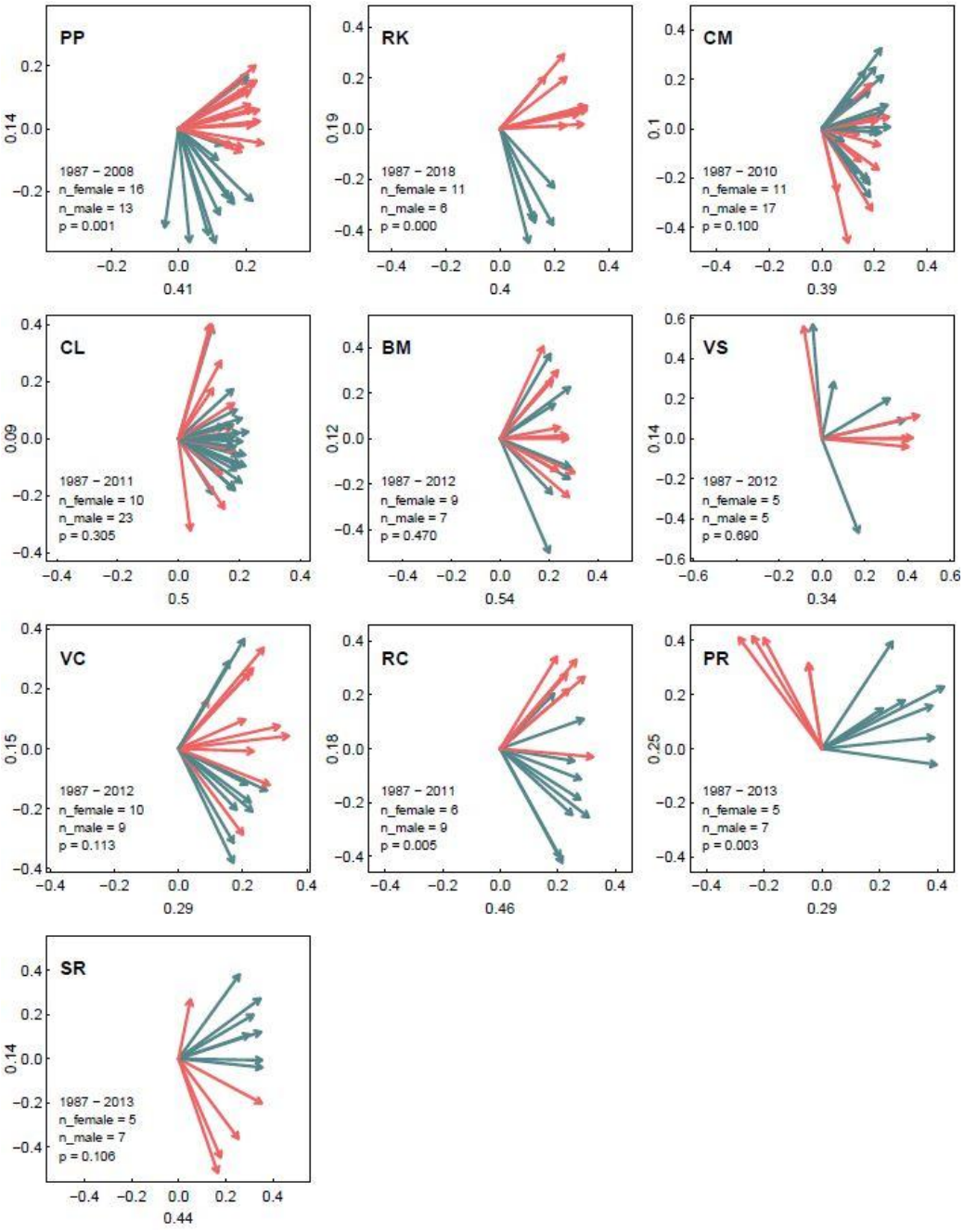


Figure 4: Spatial variation in the growth synchrony for the sex-specific RWI chronologies from each site (1987-2013). Each unfilled point shows a pairwise correlation between male (blue) and female (red) sites, and the filled points show the Mantel correlogram for male and female chronologies, and for the full site chronologies including all male and female trees (black).

3.2 Sex-specific growth patterns

PCGA demonstrated that individual trees within sites shared a strong common signal (Fig. 5). However, PCGA revealed significant sex-specific high-frequency growth variability in four sites (PP, RK, RC and PR; Fig. 5), and close-to-significant differences at further three sites. Sites with significant differences between male and female high frequency growth variability tended to have lower mean tree age, less variable growth (coefficient of variation, CV), lower within-site synchrony (rbar) and higher overall growth (mean ring width), and significant differences between male and female growth were found in xeric and mesic sites. However, with only ten sample sites

it was not possible to robustly test these associations. It was notable however, that the four sites with the strongest sex-specific high frequency growth variability (Fig. 5), also showed the strongest sex-specific growth responses to regional mast events (see Appendix A). Within each site, growth pattern between male and female trees generally showed high synchrony (mean within-site correlation of paired male and female chronologies, rh0 = 0.51; correlation of the female and male regional chronologies, rh0 = 0.62, p = 0.001, 1987-2013, Fig. 6).



277

278 Figure 5: Sex-specific differences in growth variability according to PCGA (PC1 and
279 PC2). Red arrows indicate female individuals and blue arrows indicate male individuals.
280 For each site, PCGA was conducted on individuals for the post-1987 period of the
281 chronology. Individuals that did not reach the end of the chronology were excluded, as
282 PCGA requires all individuals to have complete data over the entire testing period. *p*-
283 values are based on Wilcoxon rank tests.

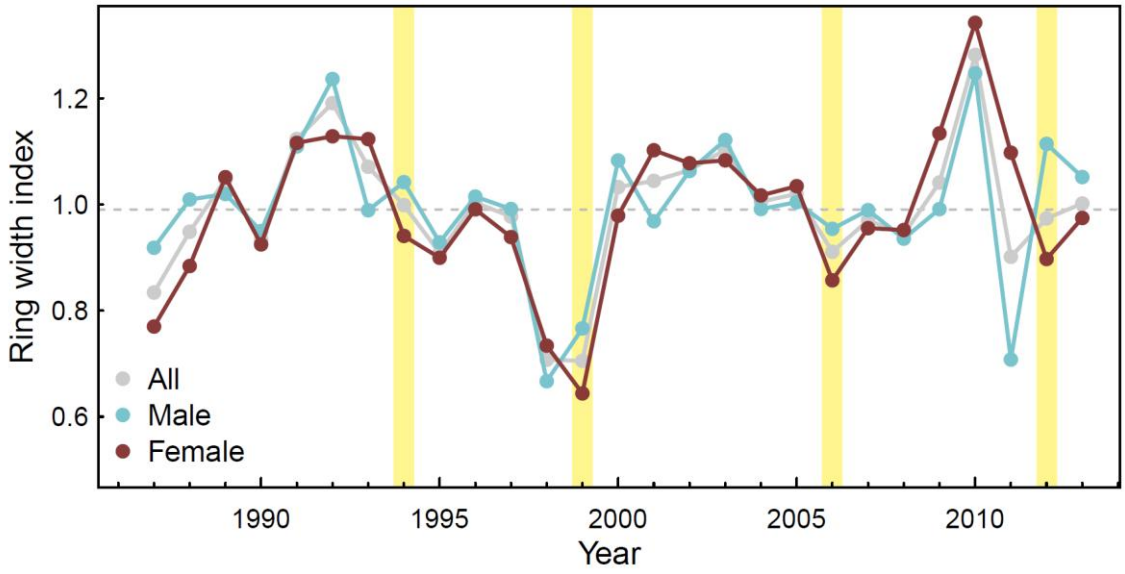


Figure 6: Ring width index of female, male and regional chronologies for the period 1987-2013. Shading indicates regional mast events.

3.3 Sex-specific growth-mast event relationships

The narrowest tree ring of the full regional chronology (including all male and female trees) was associated with the mast events in 1999, but overall, growth of the combined male and female chronology was not significantly lower in mast years than non-mast events ($t = -1.547$, $p = 0.200$). Indeed, in the mast events of 1994 and 2012, growth was close to the long-term average.

In female trees, a mast event was associated with significantly lower growth (-15.42% compared to the l987-2013 mean, significance estimated by bootstrapped resampling, Fig. 7B). This growth reduction was restricted to a single year, with close-to-normal growth in the years before and after seedfall. In males, a similar growth response was observed (-15.38%), but shifted by one year, with the significant growth anomaly associated with the year of pollination immediately prior to a mast event (Fig. 7B). Growth of male trees returned to close-to-normal levels the following year (the year of seedfall, associated with low growth in females). In both males and females,

growth was higher one and two years prior to a mast event, respectively, coinciding with the years immediately prior to pollination and flowering. The sex-specific growth responses in association with mast events resulted in a particularly strong and distinct signal in a RWI_{male}-RWI_{female} chronology (Fig. 7C). Mast events were associated with a highly distinctive sequence of a significantly negative anomaly followed by a significantly positive anomaly in the RWI_{male}-RWI_{female} chronology (Fig. 7C).

As our dataset included only four mast events and could be sensitive to the effect of individual cases of a randomly associated mast event and low growth, we re-ran all analysis excluding one mast event each time, and found consistent results. Figure 7A also supports the robustness of our results, demonstrating variation in the strength of the male-female differences between mast events, but also demonstrating that all four observed mast events (seedfall) are associated with reduced female growth relative to males, and vice-versa for the associated year of pollination.

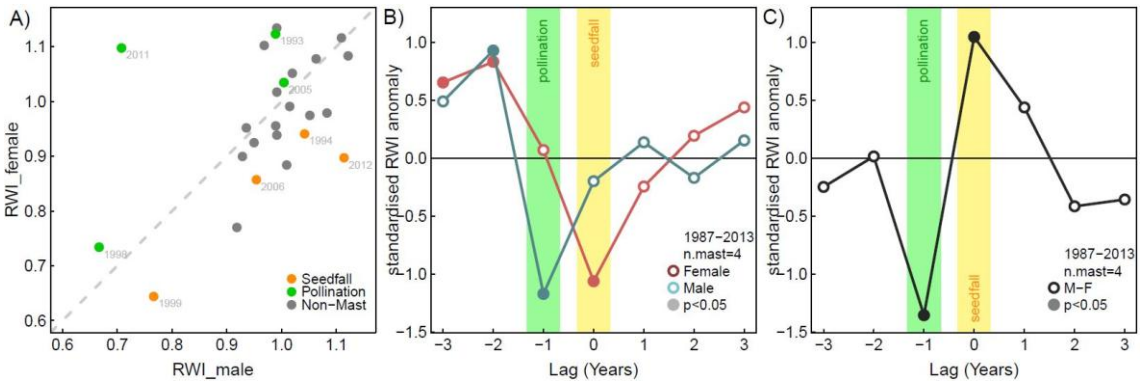


Figure 7: Regional sex-specific growth patterns associated with masting (for each site see Appendix A). A) Relationship between male and female RWI (1987-2013) according to reproductive state (pollination and seedfall years, corresponding to the four large regional masting events). B) Superimposed epoch analysis showing the response of male (blue) and female (red) RWI to mast events during the period 1987-2013. Lag = 0 is the year of seedfall, and lag = -1 is the year of pollination. Filled circles indicate

significant values at $p < 0.05$. C) Superimposed epoch analysis (SEA) showing the response of the RWI_{male}-RWI_{female} chronology to mast events during the period 1987-2013. Lag = 0 is the year of seedfall, and lag = -1 is the year of pollination. Filled circles indicate significant values at $p < 0.05$. (SEAs of each site are shown in Appendix A).

3.4 Large-scale climate controls on growth

Both female and male chronologies showed positive and significant spatial correlations with the growing season tropical SSTs ($p < 0.05$) over two years before (-2) the tree growth. Correlations were higher for female trees (Fig. 8A) than for male trees (Fig. 8B). Male and female RWI were weakly correlated with SST in the previous growing season (-1). However, female chronology showed a slightly positive, but not significant correlation with SST for the El Niño 3.4 region. In contrast, growth was generally negatively and significantly ($p < 0.05$) correlated with tropical and subtropical SSTs in the year of growth for female trees, with the highest correlations towards sectors of the sub-equatorial Pacific and near the mid latitude coast of the South American continent in the current period (Fig. 8 E-F). The correlation fields for male and female chronologies showed broadly similar patterns, but correlations with SST were stronger for the female chronology. Positive correlations were evident towards higher latitudes of the Pacific, with an apparent spatial coherence of this pattern for both female and male trees.

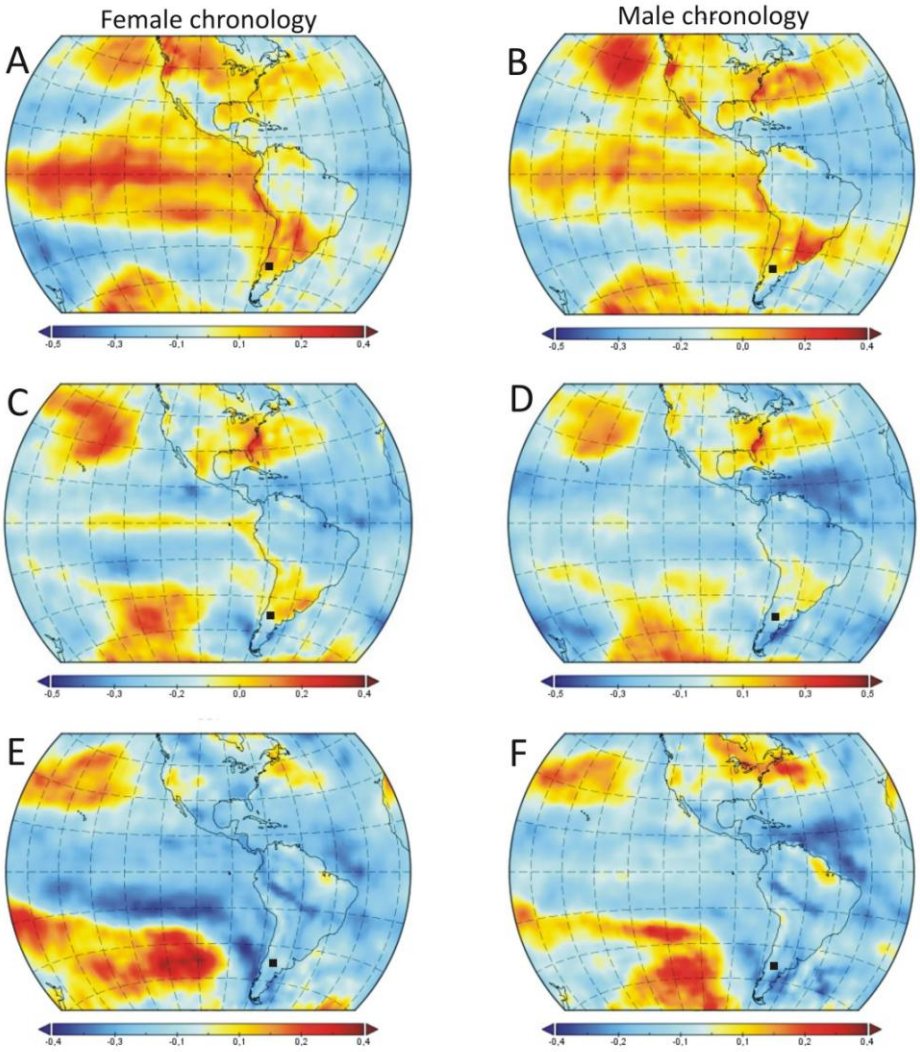


Figure 8: Spatial correlation coefficient fields (Pearson's correlation) between female (left panel) and male (right panel) regional RWI chronologies and Pacific Sea Surface Temperature (SST) and land surface temperature. A-B) correlations with the two previous growing season (Oct-Mar) SSTs, C-D) correlations with the previous growing season (Oct-Mar) SSTs, and E-F) correlations with the current growing season SST. Correlations were calculated for the period 1948-2013. Black squares indicate the study region. Significance intervals for $p < 0.05$ are < -0.242 and > 0.242, respectively. Maps were created using the spatial correlation tools provided by the NOAA/ESRL Physical Sciences Laboratory, Boulder Colorado from its website at http://www.esrl.noaa.gov/psd/data/correlation/.

4. Discussion

4.1. Sex-specific growth patterns and growth-mast event relationships

Beyond the broad spatial similarity observed between different sex chronologies, our study identified distinct sex-specific growth patterns at individual, site and regional level. This is consistent with previous studies performed with *A. araucana* (Hadad and Roig, 2016; Rozas et al., 2019), and other dioecious tree species (*Juniperus thurifera* L.; Rozas et al., 2009). We showed, for the first time, that these sex-specific growth patterns were linked to differences in the growth response of male and female trees in relation to mast events. In association with a mast event, growth was significantly reduced in female trees (which bear the seed cone), while growth was significantly reduced in male trees in the year prior to a mast event, in association with high male investment in pollen cones (the reproductive cycle of *A. araucana* occurs over two years). We interpreted these growth reductions as representing resource switching or a trade-off between growth and reproduction (Monks and Kelly, 2006; Müller-Haubold et al., 2013). However, we noted that while growth was always reduced during mast events compared to the previous years of growth, albeit offset by one year in males, (Fig. 6 and Fig. 7B), not all narrow tree rings were associated with mast events, and growth reductions associated with mast events varied substantially in magnitude (Fig. 6). This may have resulted from interactions between mast events and growing conditions during the ring formation (Hacket-Pain et al., 2017, 2019), or the status of internal reserves which may buffer any trade-off between growth and reproduction (Mund et al., 2020). In our regional RWI chronology, the absolute growth response to mast event was variable between the four mast events, however the response of male and female trees relative to each other was notably consistent. In the pollination year prior to a mast event, the growth of males was always lower than females, even when

379 the absolute growth rate was close to normal (e.g., the mast event in 1994). In the
380 following mast year, the relative growth performance of males and females was always
381 reversed, such that female growth was lower than males, again even when absolute
382 growth was close to normal. This "natural experiment" in a dioecious species where the
383 main costs of reproduction occur in different years for males and females, as in *A.*
384 *araucana*, provides a powerful tool to disentangle the effects of mast events and
385 coincident climate variability (Drobyshev et al., 2014). In our study this is shown by the
386 distinct response of a RWI_{male}-RWI_{female} chronology (Fig. 7C).

387 On the other hand, we noted that while we found strong results in regional
388 chronologies, some sites showed stronger sex-specific growth patterns than others (Fig.
389 4). Expansion of our tree-ring network and analysis of intra-annual growth features (e.g.
390 wood density, early/latewood proportions) of male and female trees may help to explain
391 why some sites did not show the strong sex-specific growth and mast responses that
392 were clear in the regional tree-ring chronology (Fig. 5, Appendix A). These mast event-
393 insensitive chronologies tended to be from sites with older trees, and presented lower
394 and more synchronised growth with higher interannual variability, perhaps indicating
395 greater effects of growth limiting factors.

396 **4.2. Sex-specific growth responses to climate**

397 Our results showed broadly similar responses of male and female chronologies to
398 variation in Pacific SSTs during the growing season months. We found that growth of
399 males and females was positively correlated with SSTs two years prior to growth, with
400 slightly stronger correlations for female trees. This lag in the effect of the climate on
401 tree growth is commonly observed in many species (Fritts, 1976). The climate
402 conditions in northern Patagonia are strongly coupled with the El Niño–Southern
403 Oscillation (ENSO) (Garreaud et al., 2009). The occurrence of warm (El Niño) events in

404 the tropical Pacific is associated with a decrease (increase) temperature (precipitation)
405 during austral spring months (September to November) and an increase (decrease)
406 temperature (precipitation) during the summer months (December to February) in north
407 Patagonia (Montecinos and Aceituno, 2003; Garreaud et al., 2009). Generally opposite
408 conditions are observed during La Niña events (Garreaud et al., 2009). Therefore, the
409 positive correlation observed between tree growth and SSTs could indicate a positive
410 relationship between *A. araucana* growth and spring precipitation two years prior to the
411 current growth period, indicating a possible interaction of growth with El Niño
412 conditions in the tropical Pacific. Furthermore, we found weak correlations between
413 growth and SST in the previous year, consistent with Mundo et al. (2012) who also
414 reported a weak negative correlation between *A. araucana* tree regional growth and sea
415 surface temperature in the El Niño Southern Oscillation (ENSO) 3.4 region in the
416 previous growing season, although they did not test this for males and females
417 separately. Our results showed that female trees had a slightly positive, but not
418 significant correlation with equatorial SST in the previous year, a response not detected
419 in the male chronology. In contrast, cold SSTs, that are linked to La Niña events, during
420 the current growing season were associated with lower growth in both male and female
421 trees, although the correlation was stronger for females (Fig. 8). This negative
422 correlation observed between *A. araucana* growth and tropical SSTs could be associated
423 with high temperatures during spring and lower precipitations during summer months
424 for the current period. Thus, growth responses to broad-scale climate controls appeared
425 to be sex-specific, as was also reported by Rozas et al. (2019) for *A. araucana* forests
426 growing on the windward side of the Andes. Other studies also reported differences in
427 growth-climate relationships in dioecious species (*J. thurifera*; Rozas et al., 2009). In
428 this sense, male trees are frequently reported to have higher drought tolerance than

429 female ones (Montesinos et al., 2012, Rozas et al., 2009). This is consistent with our
430 results where females were more strongly negatively correlated with SSTs during the
431 period of ring formation. This may result from higher water use efficiency in males
432 (Montesinos et al., 2012). Although not tested in our current analyses, we propose that
433 differences in growth sensitivity to climate between male and female trees may also
434 partly result from the interplay of climate, mast events and sex-specific costs of
435 reproduction, either where climate acts as a cue for mast years (Hacket-Pain et al.,
436 2018), or where growing season climate interacts with coincident reproductive
437 investment to influence tree growth (Hacket-Pain et al., 2017). Indeed, gender
438 differences in growth are often increased under stressful conditions (Verdu et al., 2004).

439 **4.3 Implications for mast events and climate reconstructions**

440 Long observation records of mast events rarely exceed several decades in length,
441 but such datasets provide the key to identifying long-term changes in mast events and
442 the drivers of such changes (Pearse et al., 2017; Ascoli et al., 2019). Several attempts
443 have been made to extend observational mast events records using tree-rings (Speer,
444 2001; Drobyshev et al., 2014), but these efforts have been hampered by weak mast
445 event signals in chronologies (Speer, 2001; Hacket-Pain et al., 2019, Koenig et al.,
446 2020), or difficulties in distinguishing between the signature of mast events and climate
447 (Drobyshev et al., 2014). Our results indicate that sex-specific responses to mast events
448 in dioecious *A. araucana* tree species offer a potential methodology for tree-ring-based
449 mast reconstructions, which could be extend over multiple centuries. Particularly, the
450 distinct difference of relative growth between male and female trees in the year of
451 pollination and seed fall may provide a method to distinguish mast years from other
452 non-mast growth decreases (Drobyshev et al., 2014). Although our results are regionally
453 consistent, we note that important uncertainties remain to be solved, including

454 understanding the observed between-site growth sensitivity to mast events, and the
455 potential effect of changes in tree age and/or size on the masting signal (Hadad et al.,
456 2015; Hadad and Roig, 2016; Rozas et al., 2019; Bogdziewicz et al., 2020). This
457 method would only be applicable to dioecious species, but important masting species
458 could be also studied including species of the genus *Juniperus* and the masting
459 dioecious podocarps of New Zealand such as *Dacrydium cupressinum* (Norton and
460 Kelly, 1988).

461 **5. Conclusions**

462 Male and female *A. araucana* tree-ring chronologies share a strong common
463 signal and are strongly regionally correlated. Nevertheless, we have demonstrated that
464 contrasting growth responses of male and female trees to regional mast years are
465 responsible for distinct sex-specific growth variability in this dioecious species. Growth
466 of male and female trees is reduced in response to mast events, but in different years.
467 Complementary studies are now required to establish whether sex-specific climate-
468 growth relationships in this species result from an interplay with mast events, requiring
469 the identification of the climatic cues that act to synchronise *Araucaria* mast events at a
470 regional scale. Furthermore, our results provide a framework for future work to
471 reconstruct *A. araucana* mast events over multiple decades or centuries. This would
472 improve understanding of the regeneration dynamics of this endangered species.
473 Furthermore, we argue that the ability to isolate mast events signals in tree-ring
474 chronologies can provide the basis for improving dendroclimatic calibration in *A.*
475 *araucana* trees.

476 **Author contribution statement**

477 Martín A. Hadad: Conceptualization, Methodology design, Provision of data,
478 Investigation, Data analysis, Writing - original draft, review & editing. Andrew Hacket-

Pain: Conceptualization, Methodology design, Investigation, Data analysis, Writing - original draft, review & editing. Fidel A. Roig: Conceptualization, Supervision, Writing - original draft, review & editing. Julieta G. Arco Molina: Provision of data, Writing - review & editing.

Disclosure statement

No potential conflict of interest was reported by the authors.

Acknowledgments

This research was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) through a doctoral fellowship granted to MAH and JGAM, by the Agencia Nacional de Promoción Científica y Tecnológica (PICT-Bicentenario 2010-2679 and PICT-2014-0915 to FAR and MAH, respectively). AHP and FAR acknowledge funding from The Royal Society (IEC\R2\192030). We thank Dr. Daniel Flores for the design of Figure 1. We would also like to thank private landowners and the National Park Administration (APN) for allowing access to the sites. We thank Prof. Dave Kelly for providing helpful information on masting in the dioecious podocarps of New Zealand.

Funding

MAH, FAR and AHP acknowledge the partial support from research grant Programa Cooperación Bilateral CONICET-Royal Society 2019. Part of this work was supported by Agencia Nacional de Promoción Científica y Tecnológica-Argentina (ANPCyT) by Grant 2010/2679 to FAR and 2014/0915 to MH. AHP was supported by The Royal Society grant reference for IEC\R2\192030.

Appendix A. Supplementary data

References

Aguilera-Betti, I., Muñoz, A., Stahle, D., Figueroa, G., Duarte, F., González-Reyes, Á., Christie, D., Lara, A., González, M.E., Sheppard, P.R., Sauchyn, D., Moreira-Muñoz, A., Toledo-Guerrero, I., Olea, M., Apaz, P., Fernandez, A., 2017. The first millennium-age *Araucaria araucana* in Patagonia. Tree-Ring Res. 73, 53-56.

Arco Molina, J.G., Helle, G., Hadad, M.A., Roig, F.A., 2019. Variations in the intrinsic water-use efficiency of north Patagonian forests under a present climate change scenario: Tree age, site conditions and long-term environmental effects. Tree Physiol. 39, 661-678.

Ascoli, D., Hacket-Pain, A., LaMontagne, J. M., Cardil, A., Conedera, M., Maringer, J., Motta, R., Pearse, I. S., Vacchiano, G., 2019. Climate teleconnections synchronize *Picea glauca* masting and fire disturbance: Evidence for a fire-related form of environmental prediction. J. Ecol. 12. https://doi.org/10.1111/1365-2745.13308.

Bjornstad, O.N., 2015. ncf: Spatial Nonparametric Covariance Functions. R package version 1.1-6. [WWW document] URL https://CRAN.R-project.org/package= ncf.

Bogdziewicz, M., Szymkowiak, J., Calama, R., Crone, E.E., Espelta,J.M., Lesica, P., Marino, S., Steele, M.A., Tenhumberg, B., Tyre, A., Żywiec, M., Kelly, D., 2020. Does masting scale with plant size? High reproductive variability and low synchrony in small and unproductive individuals. 126, 971-979.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia. 26, 115-124.

Bunn, A., Korpela, M., Biond, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., Buras, A., Cecile, J., Mudelsee, M., Schulz, M., 2019. Dendrochronology Program Library in R. R package version 1.6.2. http://CRAN.R-project.org/package=dplR.

Buras, A., Van Der Maaten-Theunissen, M., Van Der Maaten, E., Ahlgrimm, S., Hermann, P., Simard, S., Heinrich, I., Helle, G., Unterseher, M., Schnittler, M.,

Eusemann, P., Wilmking, M., 2016. Tuning the voices of a choir: Detecting ecological gradients in time-series populations. PLoS ONE, 11. e0158346, https://doi.org/10.1371/journal.pone.0158346.

Buras, A., Schunk, C., Zeitrg, C., Herrmann, C., Kaiser, L., Lemme, H., Straub, C., Taeger, S., Gößwein, S., Klemmt, H.-J., Menzel, A., 2018. Are Scots pine forest edges particularly prone to drought-induced mortality?. Environ. Res. Lett., 13 (2). 025001. https://doi.org/10.1088/1748-9326/aaa0b4.

Del Fueyo, G., Caccavari, M.A., Dome, E.A., 2008. Morphology and structure of the pollen cone and pollen grain of the Araucaria species from Argentina. Biocell 32, 49-60.

Deser, C., Alexander, M. A., Xie, S.-P., Phillips, A.S., 2010. Sea surface temperature variability: Patterns and mechanisms. Annu. Rev. Mar. Sci. 2, 115-143.

Donoso, C., 2006. Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología. Valdivia, Chile. Marisa Cuneo Ediciones. 678 pp.

Donoso, S., Schmidt, H., Peña, K., Perry, F., 2009. Bosques de Araucanía, producción de piñones y sustentabilidad. In: Lizana, L.A. (Ed.), *Araucaria araucana* (Mol.) K. Koch. Un Recurso Promisorio. Serie Ciencias Agronómicas Nº 15. Universidad de Chile, pp. 5-27.

Drobyshev, I., Niklasson, M., Mazerolle, M.J., Bergeron, Y., 2014. Reconstruction of a 253-year long mast record of European beech reveals its association with large scale temperature variability and no long-term trend in mast frequencies. Agric. For. Meteorl. 192, 9-17.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302-4315.

Fritts, H., 1976. Tree-Rings and Climate. Academic Press. London, England. 490 pp.

Garreaud, R.D., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day South American climate. Palaeogeogr., Palaeoclimatol., Palaeoecol. 281, 180-195.

Grissino-Mayer, H.D., 1995. Tree-ring reconstructions of climate and fire at El Malpais National Monument, New Mexico. PhD Dissertation, University of Arizona, Tucson, 407 pp.

Gut, U., Árvai, M., Bijak, S., Camarero, J.J., Cedro, A., Cruz-García, R., Garamszegi, B., Hacket-Pain, A., Hevia, A., Huang, W., Isaac-Renton, M., Kaczka, R.J., Kazimirović, M., Kędziora, W., Kern, Z., Klisz, M., Kolář, T., Körner, M., Kuznetsova, V., Montwé, D., Petritan, A.M., Petritan, I.C., Plavcová, L., Rehschuh, R., Rocha, E., Rybníček, M., Sánchez-Salguero, R., Schröder, J., Schwab, N., Stajić, B., Tomusiak, R., Wilmking, M., Sass-Klaassen, U., Buras, A., 2019. No systematic effects of sampling direction on climate-growth relationships in a large-scale, multi-species tree-ring data set. Dendrochronologia. 57, 125624, https://doi.org/10.1016/j.dendro.2019.125624.

Hadad, M.A., Roig Juñent, F.A., Boninsegna, J., Patón, D., 2015. Age effects on the climatic signal in *Araucaria araucana* from xeric sites in Patagonia, Argentina. Plant. Ecol. Divers. 8, 343-351.

Hadad, M.A., Roig F.A., 2016. Sex-related climate sensitivity of *Araucaria araucana* Patagonian forest-steppe ecotone. For. Ecol. Manag. 362, 130-141.

Hadad, M.A., Arco Molina, J.G., Roig, F.A., 2020. Dendrochronological study of the xeric and mesic *Araucaria araucana* forests of northern Patagonia: implications for the ecology and conservation, in: Pompa-García, M., J.J. Camarero-Martínez (Eds), Latin American Dendroecology - Combining tree-ring sciences and ecology in a mega diverse territory. Springer Nature, https://doi.org/10.1007/978-3-030-36930-9_13.

578 Hacket-Pain, A.J., Lageard, J.G.A., Thomas, P.A., 2017. Drought and reproductive
579 effort interact to control growth of a temperate broadleaved tree species (*Fagus*
580 *sylvatica*). Tree Physiol. 37, 744-754.
581 Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M.,
582 Drobyshev, I., Dorado Liñán, I., Friend, A.D., Grabner, M., Hartl, I., Kreyling, J.,
583 Lebourgeois, F., Levanič, T., Menzel, A., van der Maaten, E., Van der Maaten-
584 Theunissen, M., Muffler, L., Motta, R., Roibu, C., Popa, I., Scharnweber, T., Weigel,
585 R., Wilmking, M., Zang, C.S., 2018. Climatically controlled reproduction drives
586 interannual growth variability in a temperate tree species. Ecol. Lett. 21, 1833-1844.
587 Hacket-Pain, A., Ascoli, D., Berretti, R., Mencuccini, M., Motta, R., Nola, P., Piussi, P.,
588 Ruffinatto, F., Vacchiano, G., 2019. Temperature and masting control Norway
589 spruce growth, but with high individual tree variability. For. Ecol. Manag. 438, 142-
590 150.
591 Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and
592 measurement. Tree-Ring Bull. 43, 69-75.
593 Huesser, C.J., Rabassa, J., Brandani, A., Stuckenrath, R., 1988. Late-holocene
594 vegetation of the Andean Araucaria region, Province of Neuquén, Argentina. Mt.
595 Res. Dev. 8, 53-63.
596 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iridell, M.,
597 Saha, S., White, G., Woolen, J., Zhu, Y., Leetmaa, A., Reynolds, R., Chelliah, M.,
598 Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J.,
599 Jenne, R., Joseph, D., 1996. The NCEP/NCAR 40-Year Reanalysis Project. Bull.
600 Amer. Meteor. Soc. 77, 437-471.
601 Kelly, D., 1994. The evolutionary ecology of mast seeding. Trends Ecol. Evol. 9, 465-
602 470.

603 Koenig, W.D., Knops, J.M.H., Carmen, W.J., 2020. Can mast history be inferred from
604 radial growth? A test using five species of California oaks. For. Ecol. Manag. 472,
605 118233. https://doi.org/10.1016/j.foreco.2020.118233.
606 Lauder, J.D., Moran, E.V., Hart, S.J., 2019. Fight or Flight? Tradeoffs between drought
607 defense and reproduction in conifers. Tree Physiol. 39, 1071-1085.
608 McPhaden, M.J., Zebiak, S.E., Glantz, M.H., 2006. ENSO as an integrating concept in
609 earth science. Science 314, 1740-1745.
610 Monks, A., Kelly, D., 2006. Testing the resource-matching hypothesis in the mast
611 seeding tree *Nothofagus truncata* (Fagaceae). Austral Ecology 31, 366-375.
612 Montaldo, P., 1974. La bioecología de la *Araucaria araucana* (Mol.) C. Koch. Boletín
613 46/48, Instituto Forestal Latinoamericano de Investigaciones y Capacitación, Mérida,
614 Venezuela. pp. 03-55.
615 Montecinos, A., Aceituno, P., 2003. Seasonality of the ENSO related rainfall variability
616 in central Chile and associated circulation anomalies. J. Clim. 16, 281-296.
617 Montesinos, D., Villar-Salvador, P., García-Fayos, P., Verdú, M., 2012. Genders in
618 *Juniperus thurifera* have different functional responses to variations in nutrient
619 availability. New Phytol. 193, 705-712.
620 Mund, M., Herbst, M., Knohl, A, Matthäus, B., Schumacher, J., Schall, P., Siebicke, L.,
621 Tamrakar, R., Ammer, C., 2020. It is not just a 'trade-off' -indications for sink- and
622 source-limitation to vegetative and regenerative growth in an old-growth beech
623 forest. New Phytol. https://doi.org/10.1111/nph.16408.
624 Mundo, I., Roig Juñent, F.A., Villalba, R., Kitzberger, T., Barrera, M.D., 2012.
625 *Araucaria araucana* tree-ring chronologies in Argentina: Spatial variations and
626 climate influences. Trees, Struct. Funct. 26, 443-458.

Müller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F., Leuschner, C., 2013. Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. Ecosystems 16, 1498-516.

Muñoz, A.A., Barichivich, J., Christie, D.A., Dorigo, W., Sauchyn, D., González- Reyes, Á., Villalba, R., Lara, A., Riquelme, N., González, M.E., 2014. Patterns and drivers of *Araucaria araucana* forest growth along a biophysical gradient in the northern Patagonian Andes: linking tree rings with satellite observations of soil moisture. Austral Ecol. 39, 158-169.

Morales, M.S., Cook, E.R., Barichivich, J., Christie, D.A., Villalba, R., LeQuesne, C., Srur, A.M., Ferrero, M.E., Gonzalez-Reyes, A., Couvreux, F., Matskovsky, V., Aravena, J.C., Lara, A., Mundo, I.A., Rojas, F., Prieto, M.R., Smerdon, J.E., Bianchi, L.O., Masiokas, M.H., Urrutia, R., Rodriguez-Catón, M., Muñoz, A.A., Rojas-Badilla, M., Alvarez, C., Lopez, L., Luckman, B., Lister, D., Harris, I., Jones, P.D., Williams, P., Velazquez, G., Aliste, D., Aguilera-Betti, I., Marcotti, E., Flores, F., Muñoz, T., Cuq, E.., Boninsegna, J.A., 2020. 600 years of South American tree rings reveal an increase in severe hydroclimatic events since mid-20th century. Proceedings of the National Academy of Sciences. 117, 16816-16823. https://doi.org/10.1073/pnas.2002411117.

Norton, D. A., Kelly, D., 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. Funct. Ecol. 2, 399-408.

Obeso, J., 2002. The costs of reproduction in plants. New Phytol. 155, 321-348.

Ortiz, P.L, Artista, M., Talavera, S., 2002. Sex ratio and reproductive effort in the dioecious *Juniperus communis* subsp. *alpina* (Suter) Celak. (Cupressaceae) along an altitudinal gradient. Ann. Bot. 89, 205-211.

652 Owens, J.N., Takaso, T., Runions, C.J., 1998. Pollination in conifers. Trends Plant Sci.
653 3, 479-485.
654 Pearse, I.S., Koenig, W.D., Kelly, D., 2016. Mechanisms of mast seeding: resources,
655 weather, cues, and selection. New Phytol. 212, 546-562.
656 Pearse, I.S., LaMontagne, J.M., Koenig, W.D., 2017. Inter-annual variation in seed
657 production has increased over time (1900-2014). Proc. R. Soc. B Biol. Sci. 284,
658 20171666.
659 Roig, F.A., Villalba, R., 2008. Understanding climate from Patagonian tree rings, in:
660 Rabassa, J. (Ed), Late Cenozoic of Patagonia and Tierra del Fuego. Developments in
661 Quaternary Sciences 11, 411-435.
662 Rozas, V., DeSoto, L., Olano, J., 2009. Sex-specific, age-dependent sensitivity of tree-
663 ring growth to climate in the dioecious tree *Juniperus thurifera*. New Phytol. 182,
664 687-697.
665 Rozas, V., Le Quesne, C., Rojas-Badillab, M., González-Reyes, Á., Donoso, S., Olano,
666 J.M., 2019. Climatic cues for secondary growth and cone production are sex-
667 dependent in the long-lived dioecious conifer *Araucaria araucana*. Agric. For.
668 Meteorol. 274, 132-143.
669 Sanguinetti, J., Kitzberger, T., 2008. Patterns and mechanisms of masting in the large-
670 seeded southern hemisphere conifer *Araucaria araucana*. Austral Ecol. 33, 78-87.
671 Sanguinetti, J., 2014. Producción de semillas de *Araucaria araucana* (Molina) K. Koch
672 durante 15 años en diferentes poblaciones del Parque Nacional Lanín (Neuquén-
673 Argentina). Ecol. Austral 24, 265-275.
674 Selas, V., Piovesan, G., Adams, J.M., Bernabei, M., 2002. Climatic factors controlling
675 reproduction and growth of Norway spruce in southern Norway. Can. J. For. Res. 32,
676 217-225.

677 Speer, J., 2001. Oak mast history from dendrochronology: A new technique
678 demonstrated in the Southern Appalachian region. PhD Thesis, The University of
679 Tennessee.
680 Stokes, M., Smiley, T., 1968. An Introduction to Tree-Ring Dating. Univ. Chicago
681 Press, Chicago. 73 pp.
682 Swetnam, T., 1993. Fire history and climate change in giant sequoia groves. Science
683 262, 885-889.
684 Thomas, S.C., 2011. Age-related changes in tree growth and functional biology: the role
685 of reproduction. In: Meinzer, F.C., Lachenbruch, B., Dawson, T.E. (Eds), Size-and
686 Age-Related Changes in Tree Structure and Function, Springer, Netherlands. pp. 33-
687 64.
688 Verdu, M., Villar-Salvador, P., Gracia-Fayos, P., 2004. Gender effects on the post-
689 facilitation performance of two dioecious *Juniperus* species. Funct. Ecol. 18, 87-93.
690 Villalba, R., Lara, A., Masiokas, M.H., Urrutia, R., Luckman, B.H., Marshall, G.J.,
691 Mundo, I.A., Christie, D.A., Cook, E.R., Neukom, R., Allen, K., Fenwick, P.,
692 Boninsegna, J.A., Srur, A.M., Morales, M.S., Araneo, D., Palmer, J.G., Cuq, E.,
693 Aravena, J.C., Holz, A., LeQuesne, C., 2012. Unusual Southern Hemisphere tree
694 growth patterns induced by changes in the Southern Annular Mode. Nature Geosci.
695 5, 793-798. https://doi.org/10.1038/ngeo1613.
696